

The problem of allocation of fossil land shells to the proper genera has been difficult for paleontologists to solve. The temptation is strong to create new group names without tangible morphological characters and solely on the basis of geologic or geographic position of the specimens. However, it seems best in this regard, when no pronounced structural differences can be found, to follow the work of such authors as Pilsbry,⁷ Cockerell and Henderson and refer the species to the genus which lives in the region today.

⁷ PILSBRY, H. A., *Manual of Conchology*, ser. 2, vol. 9, p. XLIV. 1894.

PALEONTOLOGY.—*Pleurotomaria pseudostrigillata* *nom. nov.* and *Chonetes acanthophorus* *nom. nov.*¹ GEORGE H. GIRTY, U. S. Geological Survey.

In the course of describing the Guadalupian fauna in 1908² I unwittingly named one of the species *Pleurotomaria strigillata*, overlooking the fact that Herrick³ had already described a Waverly species under that name. The Guadalupian species should now be known as *Pleurotomaria pseudostrigillata*. Furthermore, Mr. Ralph H. King has considerably called my attention to the circumstance that my *Chonetes granulifer* var. *armatus*⁴ is virtually a homonym of *Chonetes armatus*⁵ Norwood and Pratten 1854, a name even at that time preoccupied by Bouchard.⁶ I propose to substitute *Chonetes acanthophorus* for the form found in the Wewoka formation. Acknowledgment for some of these references is gratefully made to Mr. King.

¹ Published by permission of the Director of the U. S. Geological survey. Received November 8, 1934.

² U. S. Geol. Survey Prof. Paper 58: *pl. 24, figs. 21, 21a.* 1908.

³ Bull. Sc. Lab. Denison Univ. 3: 86, *pl. 1, figs. 10, 15; pl. 2, fig. 25.* 1888.

⁴ U. S. Geol. Survey Bull. 544: 62, *pl. 7, figs. 2-4.* 1915.

⁵ Acad. Nat. Sci. Philadelphia Jour. 3: 28. 1854.

⁶ See MURCHISON, DE VERNEUIL, and KEYSERLING, *Geologie de la Russie*, etc. 2: 241. 1845.

BOTANY.—*The inflorescence in Schizostachyum Nees.*¹ F. A. MCCLURE, Lingnan University. (Communicated by A. S. HITCHCOCK.)

During the course of a study of the Chinese species of *Schizostachyum* just completed,² it became apparent to the writer from a comparison of numerous herbarium specimens with their published descriptions, and from a study of various published descriptions of the genus, that the structure of the inflorescence is not as well understood as it should be. Reasons for this are not difficult to find. The fluid and unusual nature of the inflorescence in this genus has caused no

¹ Received July 27, 1934.

² To appear shortly in the Lingnan Science Journal.

end of confusion, and the terminology used in the descriptions has, almost without exception, been inconsistent and misleading, largely because of faulty interpretations of the component structures.³

Although Nees (1829) made allusion, in the name of the genus,⁴ to one of its fundamental characters, it would seem, judging from his description, that he did not himself fully comprehend the significance of the character in terms of the morphology of the inflorescence.

The genus was briefly described by Nees on the basis of a single species collected by Blume in Java. When Ruprecht (1839) prepared his monograph two additional species were recognized. Ruprecht revealed a sense of dissatisfaction with Nees's terminology as well as an uncertainty as to the correctness of his own, and for the most part his description of the genus shows little improvement over Nees's. In fact, among other errors he made the mistake of calling the spikelets 3-flowered. Nevertheless, in a footnote (op. cit., p. 134) he arrives at a statement "*Glumae in descr. Neesii sunt nostrae valvulae florum (in icone) vel rectius bractee spiculas vel gemmas includentes . . .*" (italics mine), which points the way to a better understanding of the inflorescence. Judging from the terminology of subsequent descriptions, however, no one seems to have given any serious attention to this hint.

Nees's original description of the genus (op. cit., p. 535) together with an emended description prepared by the writer on the basis of a study of the Chinese species, will provide a background for the discussion that follows.

SCHIZOSTACHYUM †

"Spiculae teretiusculae, glomerato-spicatae, inferne compositae interjectis inter glumas pedicellis sterilibus, uniflorae. Glumae inferiores alternatim minores, aequinerviae; superiores tres aut quatuor majores, circumvolutae, aequinerviae, quarum suprema sola fertilis. Valvulae distinctae nullae (nisi supremae squamas glumiformes valvulas existimes). Lodiculae nullae. Stamina sex, antheris linearibus erectis. Stylus simplex, longus; stigmata tria, pubescentia. Caryopsis ignota.

"Inflorescentia: spicae terminales ramorum approximatae, simplices. Spiculae in glomerulos dissitos congestae, spathis scariosis variis suffultae et interstinctae. Gramina vere bambusoidea, arborescentia, foliis petiolatis."

SCHIZOSTACHYUM BLUMII †

"Species una nobis cognita, foliis est fere pedibus oblongo-lanceolatis acuminatis glabris, vaginis ore nudis, ligula brevissima.

"Habitat in Java Insula: cl. Blume.

³ It is probable that the neglect of the prophylls as constituting a category distinct from the bracts and glumes, and the consequent failure to use them as orienting structures, are largely responsible for this faulty interpretation.

⁴ From the Greek: *σχίζειν* = split, and *σπίκη* = spike.

“Adnot. Genus Beesha Kunth., Melocana [sic!] Tr. (*Bambusa baccifera*, Roxb. (*Beesha Rheed. H. Mal. V. t. 60*), nostro quoad spiculas proximum, differt inflorescentia, valvulis (si modo recte observata sint a scriptoribus) diversa forma distinguendis, fructu bacciformi.”

The following is the writer's characterization of the genus based on a study of the Chinese species.⁵

SCHIZOSTACHYUM Nees emend.

CLUMP HABIT dense or open; RHIZOME sympodial,⁶ with a tendency in some forms to run a little distance laterally before turning upward to form the culm, thus giving rise to a more open clump habit; CULMS erect or ascending, terete, thin-walled, usually straight, sometimes somewhat zigzag, the tips upright, drooping, or clambering; *nodes* not prominent, but usually bearing a narrow ring of pithy tissue left from the base of the deciduous sheaths; *internodes* cylindrical, each smooth and shining at its base, the remaining portion with a siliceous covering which increases in thickness toward the summit of the internode, the siliceous part at first variously strewn with brittle, appressed, acicular hairs, ultimately more or less glabrescent, a zone of varying width just below the nodes usually being somewhat glaucous, more densely covered with these hairs, and more tardily glabrescent; *prophylls* (at culm nodes) ovate, obtuse, flat, shining, each containing numerous (up to 10) buds⁷; BRANCHES numerous, subequal, in fascicles, slender, the basal 2 to 6 internodes short, closely clothed with short, more or less persistent, imbricate sheaths, each sheath usually bearing in its axil a prophyll containing dormant or active buds, the branches rarely rebranching at their distal nodes; CULM SHEATHS cylindrical, convolute, coriaceous-chartaceous, usually more or less conspicuously striate or ribbed, siliceous, usually more or less covered with brittle, acicular hairs and ultimately glabrescent; *auricles* usually obsolete or nearly so; *oral setae* usually prominent; *pseudophylls* reflexed, long and narrow with involute margins and subulate tips; BLADES of widely varying size and shape, even on the same plant, acuminate, subulate or acicular, usually more or less rough to the touch on one or both surfaces, sometimes entirely glabrous on one surface or the other, always with several scabrous veins along the outer margin of the upper surface; the *margins* cartilaginous and more or less scabrous; the secondary veins on the under surface often with a tessellate appearance, especially in young leaves; INFLORESCENCES arising from solitary buds⁷ but forming clusters, often in heads when older, sometimes more lax and open, terminal or lateral on leafy or leafless branches of primary, secondary or even higher order, sometimes (in *S. dumetorum* Munro at least) borne directly on the nodes of the main culm; the *main axis* (of the inflorescence) and the *rachis branches* of all subsequent orders, short, deter-

⁵ Hitherto only 2 species have been recorded from China: *S. chinense* (a rather aberrant species, concerning the vegetative characters and habit of which little is known) and *S. dumetorum*. To these have been added *S. lima*, formerly known only from the Philippine Islands, and two newly described, apparently endemic species.

⁶ Sympodial rhizomes are short and thick, with congested nodes, and are early determinate, i.e., after growing horizontally for a short distance they turn upward to form a culm. This type of rhizome gives rise to a more or less crowded or caespitose type of clump. For a fuller definition of the meaning of this term as used by the writer, see Lingnan Agr. Rev. 3: 40-47. 1925.

⁷ The examinations were made by ordinary dissection. This point should be checked by means of serial sections of the branching structure during its young stages.

minate, ultimately much branched, the branching system being indeterminate, becoming predominantly sympodial with age, the individual rachis branches each with a prophyll at its base and completely covered, in its early stages, with crowded imbricate bracts, the terminal rachis joints elongate, with expanded apices, each bearing a 1-flowered spikelet; *prophylls* (of the inflorescence) 1-8 mm. long, triangular and obtuse to linear-lanceolate and acute, the keels white-ciliate; *bracts* 1-several, gemmiferous, ovate to sublinear, obtuse and awnless to acute and more or less definitely awned, few- to many-nerved, sometimes with the central nerve forming a keel, glabrous or variously pubescent, the upper ones approaching the lemmas in size and shape; *spikelets* 1-flowered, sessile, perfect, staminate or intermediate (rudimentary perfect), the perfect ones promptly deciduous, the intermediate ones more tardily so, and the staminate ones persistent; *glumes* entirely lacking (except in *S. chinense* Rendle); *sterile lemmas* wanting (except in *S. chinense*); *lemmas* convolute, resembling upper bracts of the pseudo-spikelets, thin-chartaceous to more or less indurate, many-nerved, obscurely to definitely awned, shorter than the palea in perfect spikelets, longer than the palea and completely enveloping it in the staminate and rudimentary perfect spikelets; *paleas* convolute, often more or less spirally twisted, soft and flexible at the base, firm above, not obviously keeled but bearing dorsally a slender rachilla-joint lying in a shallow, inconspicuous sulcus, the latter becoming wider and deeper near the notched, or more or less prominently bifid, indurate apex; *rachilla* not disarticulating (except the basal joint in *S. chinense*), the terminal joint (at back of palea) pearly-white, flattened at the base, slender, bristle-like, often tipped with a minute, bud-like or leaf-like structure (rudimentary floret?), the latter being more conspicuous in staminate spikelets; *lodicules* wanting (except in *S. chinense*); *stamens* 6 (sometimes 7), included or exerted, with flat filaments, the anthers with blunt apices and unequally bifid bases; *pistils* stipitate, with the narrow, linear ovary attenuate into a slender style terminated by usually 3, sometimes 2, plumose stigmas; *fruit* (in *S. dumetorum*; unknown for the other Chinese species) fusiform, with a long, slender beak, the coriaceous pericarp separable from the grain or seed except at the back.

The inflorescences of the Schizostachyums that have been studied by the writer are borne at the distal nodes of leafy or leafless branches of primary, secondary or even higher order, or they may sometimes be borne directly upon the nodes of the main culm. The primary buds giving rise to the inflorescences are apparently solitary, but each develops into a complicated, though usually short, branching system. The main axis and the individual branches of the rachis are more or less promptly determinate, always ending in a 1-flowered spikelet, which may be perfect, staminate, or intermediate. Moreover, there is a tendency, more obvious in older inflorescences, toward typical sympodial branching (fig. 1, A and B).

While the individual branches of the rachis are thus determinate in their development, the inflorescence as a whole is entirely indeterminate, being enlarged, or rather made more dense, by the continued development of new branches from the buds in the axils of the bracts. The writer has records which indicate definitely that in several species of this genus a given in-

florescence may produce new rachis branches and new spikelets in the second year. This behavior is apparently common to all the species studied, and it is probable that the process may go on for an even longer period than has been indicated by the records. Camus (1913) p. 173, no doubt refers to this same phenomenon when he says of *S. Zollingeri* Steud. "parfois les fascicules inférieurs prolifères."

Pilger (1927) observed the presence of a similar branching system in the

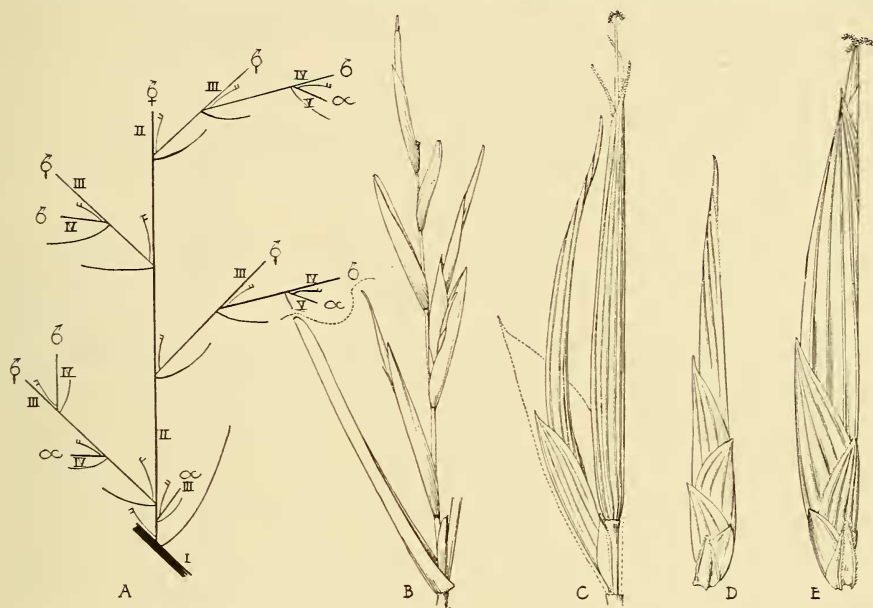


Fig. 1.—A. Diagram of an inflorescence of *Schizostachyum lima* which may be taken as typical for the genus. The Roman numerals indicate the order of the rachis branches, counting the branch from which they originated as I. ♂ indicates fully developed perfect spikelets; ♀ indicates rudimentary perfect spikelets; ♂ indicates staminate spikelets; ∞ indicates a bud or an incompletely developed branch. The bracts, and the sheath subtending the inflorescence, are indicated by simple curved lines, while the prophylls are shown as curved lines with two short lines inserted at right angles at their tips. B. A sketch of an inflorescence of *S. lima*. Some of the bracts, as well as the sheath subtending the inflorescence, have lost their pseudophylls. ×1. C. A portion of the tip of a rachis branch (pseudo-spikelet) of *S. lima* in an advanced stage of development. The lateral buds have produced branches which destroy its original spikelet-like appearance. The perfect spikelet (terminal) is supported by a short lateral branch (another little pseudo-spikelet) terminated by a staminate spikelet. The subtending bract is indicated by broken lines. ×3. D. A small pseudo-spikelet of *S. hainanense* terminated by a staminate spikelet. ×5. E. A pseudo-spikelet of *S. hainanense* terminated by a perfect spikelet. Note the 2-keeled prophyll at its base. Each of the four bracts bears in its axil a bud capable of developing into another pseudo-spikelet. ×5.

inflorescence of *Guadua tessmannii* Pilg., and Möbius (1898) recorded for *Bambusa vulgaris* Wendl. the development, in the second year of its flowering, of buds from a year-old rachis branch into new "spikelets." It is probable that this behavior is more common in other genera also than is generally suspected.

It is important to point out, at this juncture, that the fully developed perfect spikelets are rather promptly deciduous, while the rudimentary perfect ones fall much more tardily, the staminate ones being persistent. This behavior, operating along with the continuous development of new rachis branches, results in a growing preponderance, in specimens which have been flowering for some time, of imperfectly developed (or rudimentary) perfect spikelets, along with the staminate ones. In the course of ordinary handling, any remaining perfect spikelets may easily be lost, as well as many of the somewhat rudimentary ones. And when it is remembered that the shape and relative size of the component parts of the spikelet vary with the sexual state of the spikelet, it is easy to see how one may gain an entirely different impression from the examination of young inflorescences as compared with that to be gained from the examination of those which have undergone a long development.

It is an easy matter to ascertain the relative, if not the actual, age of the inflorescences of *Schizostachyums* in herbarium specimens or elsewhere. As a result of the continued development of additional branches in a system in which the main axis and all of the branches are very short, the older the inflorescence, generally speaking, the more crowded it will have become. In specimens in which flowering has continued for more than a year the contrast between the new and the old parts will be readily apparent when one looks for it. The older spikelets and structures will have a blanched appearance and be brittle, and will probably be more or less damaged, while those of the current year's growth will have a fresher, firmer appearance, and will often retain a greenish tinge. The relative number of bare rachis tips in a given inflorescence will be an index to the number of perfect spikelets that have fallen. Furthermore, it should be remembered that in fully developed perfect spikelets the palea always is exerted, however slightly, beyond the tip of the lemma. If there are no spikelets in this condition, the inflorescences are either very young (in which case there will be no naked rachis tips) or they are very old (in which case the naked rachis tips will be relatively numerous).

The branches of the rachis are covered with gemmiferous bracts.⁸ Before their buds have developed, these branches have the appearance of spikelets, for which structures they have commonly been mistaken (fig. 1, D and E). The presence, however, of a prophyll⁹ (often described as a 2-keeled glume) at the base of each, and of buds in the axils of the bracts (so-called gem-

⁸ In the very rare cases where a bud was not found in the axil of a bract, it seemed likely that, being quite small, it was overlooked or lost.

⁹ The prophyll has been largely neglected in the published descriptions of bamboos. And while it is not entirely lacking in taxonomic value, Takenouchi (1931) has perhaps over-emphasized the usefulness of its characters for distinguishing species. This structure has been of the greatest value to the writer, however, as an orienting structure leading to an understanding of the morphology of the inflorescence in *Schizostachyum*, where the small size and the extremely crowded condition of the floral structures make ordinary dissection particularly difficult. It is perhaps in connection with this aspect of bamboo study that its usefulness should be more strongly emphasized.

miferous glumes), reveals their true nature immediately.¹⁰ As soon, however, as the lateral buds of a given rachis branch have developed to any extent, it loses its spikelet-like appearance, and the terminal spikelet itself becomes more evident. In those species which have the terminal rachis joints most elongate, the true spikelet is likewise more easily discernible. In such species the terminal perfect spikelets are typically seen to be supported on one side by a short rachis branch terminated by a staminate spikelet (fig. 1, C). Camus (1913), p. 177, would seem to be referring to this condition when he says of *S. latifolium* Gamble, "Epillets . . . groupés par 2 . . ."

SUMMARY

1. The structure of the inflorescence in the genus *Schizostachyum* has been misinterpreted since its first description, and the terminology used has been inconsistent and misleading.

2. It is suggested that the neglect of the prophylls as constituting a category distinct from the bracts and glumes, and the consequent failure to use them as orienting structures are largely responsible for this faulty interpretation.

3. As a background for the discussion Nees's original description of the genus and the type species is given, along with the writer's own recently prepared emended description of the genus based on a study of the Chinese species.

4. The following sources of confusion in the interpretation of the inflorescence of *Schizostachyum* are pointed out:

a. The indeterminate nature of the inflorescence as a whole, which grows out of the successive development of additional rachis buds.

b. The unusual, spikelet-like form taken by the determinate rachis branches (pseudo-spikelets).

c. The fact that the spikelets terminating these branches of the rachis may represent any sexual state from purely staminate, through rudimentary perfect, to fully developed perfect, with corresponding discrepancies in the shape and relative size of the different component structures.

d. The fact that there may exist, in a given inflorescence at a given moment, spikelets (as well as the rachis branches which they terminate) in various stages of development.

e. The prompt deciduousness of the fully developed perfect spikelets, which leaves, in the older inflorescences, an impression that certain more tardily deciduous forms of the spikelet are representative, because most numerous.

¹⁰ As an aid in making clear the distinction between these structures and the real spikelets, the term *pseudo-spikelet* has been used, in the descriptions recently prepared by the writer, to indicate these bract-covered ultimate branches of the rachis. The proper significance of this term, as well as the modern sense of the terms *bract* and *glume*, (Chase, 1922 and Piper, 1906) should be kept in mind in comparing these with the older descriptions. The structures referred to in the existing descriptions as "glumes" or "gemmiferous glumes" are really, for the most part, *bracts*. Glumes, in the modern sense, are lacking in all the Chinese species of the genus except *S. chinense*. This species is also aberrant among the Chinese species in the possession of lodicules, a sterile lemma, and a disarticulating rachilla.

ACKNOWLEDGMENTS

The present paper is the beginning of the fruition of field work on the Chinese bamboos begun in 1921, and is based on herbarium material and notes brought together chiefly by the writer and the staff of the Lingnan University Herbarium. Full acknowledgment is made elsewhere of special financial assistance for this work received from various outside sources, but special mention is due the Rockefeller Foundation for its most recent grant, which has made possible the purchase of hitherto unavailable literature and equipment essential to the continued pursuit of this work.

The writer wishes to acknowledge his great indebtedness to Dr. A. S. Hitchcock and Mrs. Agnes Chase for assistance and advice, and for numerous courtesies in connection with the use of their unexcelled private agrostological library, and the grass collections of the United States National Herbarium.

LITERATURE CITED

- ARBER, A. *Studies in the Gramineae*. 1. *The flowers of certain Bambuseae*. Ann. Bot. 50: 463, fig. 10, F. 1926.
- BENTHAM, G. and HOOKER, J. D. *Genera Plantarum*. 3: 1214. 1883.
- BROWN, W. H. *Minor economic products of the Philippine forests*. 1: 263-265, pl. 21-33. 1920.
- CAMUS, E. G. *Les Bambusées*. 171-179, pl. 95-98. 1913.
- CAMUS, E. G. and CAMUS, A. *Graminées*, in LECOMTE, H. and GAGNEPAIN, F. *Flora generale de l'Indochine*. 7: 642-646. 1923.
- CHASE, AGNES. *First book of grasses*. 17-24. 1922.
- GAMBLE, J. S. *The Bambuseae of British India*. Ann. Roy. Bot. Gard. Calcutta. 7: 114-118, pl. 100-104. 1896.
- GAMBLE, J. S. *The bamboos of the Philippine Islands*. Philip. Journ. Sci. Bot. 5: 273-278. 1910.
- GAMBLE, J. S. *A new species of Schizostachyum*. Philip. Journ. Sci. Bot. 6: 289. 1911.
- GAMBLE, J. S. *Some additional bamboos of the Philippine Islands*. Philip. Journ. Sci. Bot. 8: 205-206. 1913.
- HACKEL, E. *Gramineae*, in ENGLER, A. and PRANTL, K. *Pflanzenfam.* 2: 97. 1887.
- HANCE, H. F. *Bambusa dumetorum*, in Walp. Ann. 3: 781. 1852-3.
- MCCLURE, F. A. *Some notes on the bamboos of Kwangtung*. Lingnan Agr. Rev. 3: 40-47, fig. 1-9. 1925.
- MOBIUS, M. *Über ein eigentümliches Blühen von Bambusa vulgaris Weendl.* Bericht. Senckenb. Nat. Ges. 1898: 81-89, pl. 4. 1898.
- MUNRO, Wm. *A monograph of the Bambusaceae*. Trans. Linn. Soc. 26: 135-138. 1868.
- NEES, C. G. *Agrostologia Brasiliensis*. 535. 1829.
- PILGER, R. *Über die Blütenstände und Ährchen der Bambuseen-Gattung Guadua Kunth*. Bericht. Deutsch. Bot. Ges. 45: 562-570, fig. 1-2. 1927.
- PIPER, C. V. *The terminology of the parts of the grass spikelet*. Science 23: 789-790. 1906.
- RENDEL, A. B. *Bambuseae*, in FORBES, B. F. and HEMSLEY, W. B. *Enumeration of all the plants known from China Proper, etc.* Journ. Linn. Soc. Bot. 36: 448-449. 1904.
- RUPRECHT, F. J. *Bambuseae*. Mem. Acad. St. Petersburg. VI. Sci. Nat. 3¹: 43-47, pl. 16 (fig. 44), pl. 17 (fig. 44 and 46). 1839.¹¹
- TAKENOUCHI, Y. *Systematisch-vergleichende Morphologie und Anatomie der Vegetationsorgane der japonischen Bambus-Arten*. Mem. Fac. Sci. Agr. Taihoku Imp. Univ. 3: 37-53, fig. 22-29, pl. 3. 1931.

¹¹ This paper was first issued in 1839 as a separate with pagination 1-74. When it appeared in the regular series in 1840 the pagination was changed to 91-164. Thus, in the latter place our reference would be pp. 133-7.